



A review of management actions on insect pollinators on public lands in the United States

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Abstract

Public lands face growing demands to provide ecosystem services, while protecting species of conservation concern, like insect pollinators. Insect pollinators are critical for the maintenance of biodiversity and ecosystem function, but it is unclear how management of public lands influence pollinator conservation. We found 63 studies investigating the effects of prescribed burning, logging, grazing, invasive species removal, revegetation with wildflower mixes, and hosting commercial pollinators, on native insect pollinators on natural and semi-natural ecosystems in the US and summarized the results across taxa and habitat types. Manual removal of invasive shrubs and revegetation with wildflower mixes had consistently positive effects on pollinators. Grazing had neutral effects on pollinators in the Great Plains, but negative effects elsewhere. Prescribed burning had neutral or positive effects for bees depending on the habitat type, with occasional negative effects on butterflies. Logging had neutral to positive effects that were more uniform across ecosystems and taxa than burning. Burning combined with logging benefited pollinators, even when burning or logging alone had no effects. Although poorly studied, hosting commercial pollinators may negatively affect wild bees through pathogen transmission and competition for floral resources. Despite the rapid accumulation of information on factors contributing to pollinator declines, the effects of management actions on pollinators remain understudied for many taxa and habitat types in the US. Improving our understanding of the effects of public land management on pollinators is essential to conserve ecosystem health and services required by society.

Keywords Conservation · Insect · Management · Pollinator

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Introduction

Pollinating insects (hereafter ‘pollinators’) are essential for the maintenance of biodiversity and functioning of ecosystems. Pollinators sustain healthy vegetation communities by facilitating reproduction of plants through the transfer of pollen between conspecific individuals (Michener 2007; Ollerton et al. 2011). Insects that pollinate plants include flies, wasps, butterflies, beetles, and moths, but bees (Hymenoptera: Apoidea) are considered the most effective pollinators for many plant groups because they actively collect pollen as their primary food source for larvae and adults (Winfree et al. 2011). However, global declines of bees (Goulson et al. 2015; Potts et al. 2010; Vanbergen and the Insect Pollinators Initiative 2013), butterflies (Powney et al. 2019), and other flying insects (Hallmann et al. 2017) threaten the delivery of pollination services in wild (Burkle et al. 2013) and agro-ecosystems (Kleijn et al. 2015; Klein et al. 2007). Beyond the effects of pollinator diversity for ecosystem function, pollinators are charismatic and culturally significant species that have intrinsic value worth protecting. Conservation measures that support insect pollinator populations are needed to preserve biodiversity and fulfill the pollination services required by society.

Public lands in the US are natural and semi-natural areas owned collectively by US citizens that span diverse habitat types including forest, grassland, shrubland, desert, and riparian areas. Within the contiguous 48 states, forests (24.41%), shrublands (21.61%), and grasslands (14.56%) are the most represented natural and semi-natural habitat types (Wickham et al. 2014). Federal land management agencies including the United States Forest Service (USFS), National Park Service (NPS), United States Fish and Wildlife Service (USFWS) and Bureau of Land Management (BLM), collectively manage 95% of all publicly owned land, comprising 245.4 million hectares of land area and 27% of the total land base of the US (U.S. Congressional Research Service 2020) (Fig. 1). Public lands are known to include some of the most species rich ecosystems for pollinators in the US (Auerbach et al. 2019; Koh et al. 2016; Wilson et al. 2018). However, most public lands in the US are managed for multiple purposes including preserving ecological integrity and cultural/historic landmarks while also provisioning goods and services for human societies such as energy, logging, grazing, recreation opportunities, and temporary agriculture. Consequently, federal land management agencies are tasked with striking a balance between preserving ecological health and producing the services and goods required for human well-being (Millennium Ecosystem Assessment 2005).

Research communities and government agencies are motivated to develop conservation strategies to counteract pollinator declines on public lands, but threats to pollinators remain unknown because land managers lack baseline population data for most species and the effects of land management actions on pollinators are rarely studied. In the US, pollinator protection has been advanced through a Presidential memorandum (Obama 2014), the formation of a pollinator health taskforce (Pollinator Health Task Force 2015), federal guidelines for pollinator conservation (e.g., pollinator-friendly best management practices), and listing some pollinator species (e.g., the rusty patched bumble bee; *Bombus affinis*) under the Endangered Species Act. However, despite recent and rapid accumulation of pollinator data and cooperation between federal agencies (Graves et al. 2020), land managers still lack baseline data for many pollinator populations (Woodard et al. 2020) and are unaware of the effects of management actions on pollinators (Hanula et al. 2016; Rivers et al. 2018a). Synthesizing information on how land management affects pollinators could help federal agencies make management decisions that are consistent with pollinator conservation.

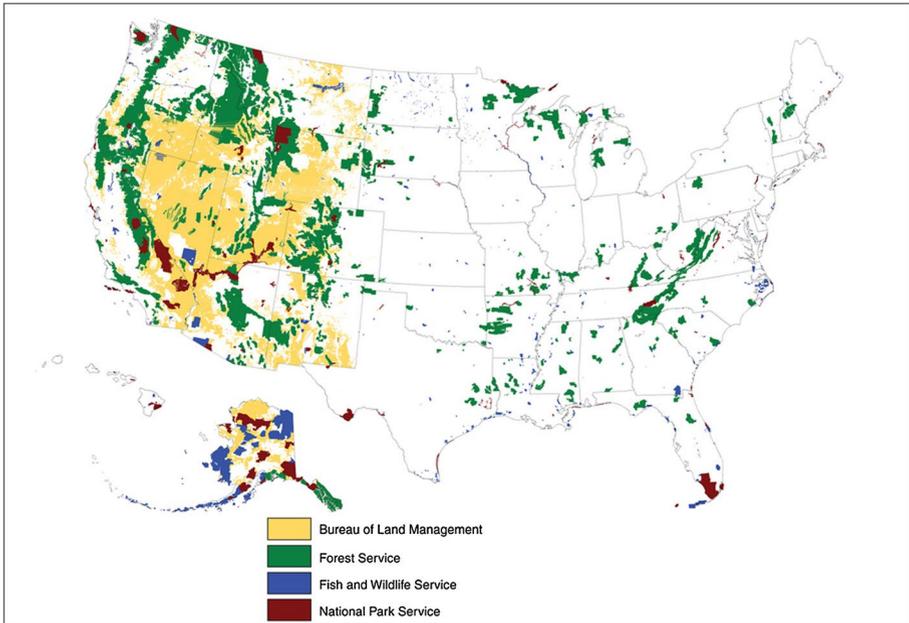


Fig. 1 Federal lands managed by the Bureau of Land Management, US Forest Service, US Fish and Wildlife Service, and National Park Service. This figure is repurposed from the US Government Accountability Office (GAO) report 11-144 (U.S. Government Accountability Office 2010)

Management actions can influence pollinators by altering the availability of foraging and nesting resources at both local and landscape scales. Locally, management actions that alter the diversity and abundance of flowering plants change the availability of dietary protein and nitrogen required to rear bee larvae and of nectar necessary to maintain metabolic rates of adult bees, butterflies, and flies (Roulston et al. 2011). Nesting substrates are also critical resources for bees but have largely been neglected as a management priority for pollinator conservation (Harmon-Threatt 2020). Most bee species are ground-nesting and require exposed, dry, malleable soils with high temperatures and high light availability, while above-ground nesting bees need resins, mud, or vegetation to construct brood cells in wood or rock cavities or hollow-stemmed plants (Harmon-Threatt 2020). For non-bee pollinators, management can modify the availability and quality of larval habitats. The larvae of many fly pollinators (e.g., Syrphidae) feed on microorganisms in dead wood or are predators of other invertebrates, like aphids (Dunn et al. 2020; Lucas et al. 2017). Furthermore, management may modify the availability of oviposition sites for butterflies by altering plant populations that are the preferred food resources for caterpillars (Smallidge and Leopold 1997). At a landscape scale, management actions increase habitat heterogeneity and provide complementary resources to support overall higher levels of pollinator abundance and diversity (Grundel et al. 2010). Management that modifies habitat important for pollinators—especially the diversity and abundance of flowering plants, amount of bare ground, and availability of dead wood—can affect pollinator abundance and diversity.

Pollinator conservation efforts have primarily been developed within agricultural and urban areas, resulting in a lack of understanding of how management on public lands can

influence pollinators. To fill this knowledge gap, we review the effects of common land management actions on pollinators and identify knowledge gaps to guide future research for pollinator conservation on public lands in the US. We summarize the effects of prescribed burning, logging, grazing, invasive species removal, revegetation with wildflower mixes, hosting commercial pollinators, and the combination of management actions on native pollinators on federally-owned semi-natural and natural systems in the US (hereafter ‘public lands’). Furthermore, our understanding of the effects of management on pollinators varies depending on the management action and habitat type. We highlight knowledge gaps and research areas needed to improve management for pollinator conservation on public lands. Results from this work can inform land managers on how to apply management actions to provision ecosystem services while conserving pollinators.

Materials and methods

Identifying common management actions on US public lands

To identify the actions that agencies are prioritizing to achieve current and future land management goals, which also can modify pollinator habitat, we reviewed the most recent drafts of land management plans for National Forest Units (NFUs). As of February 2021, 20 NFUs had land management plans available to the public (Supplemental Table 1). Within each management plan, we searched for the word ‘pollinator’ to identify all the management actions used to support pollinator habitat on public lands. Six management actions were identified: (1) prescribed burning, (2) logging, (3) grazing, (4) invasive species removal, (5) revegetation with wildflower mixes and (6) hosting commercial pollinators (e.g., honey bees) on public lands.

Literature review

We searched the Institute for Scientific Information (ISI) Web of Science database (<http://apps.webofknowledge.com>) and Google Scholar (<http://scholar.google.com>) to find studies that assessed the effects of management on pollinators on public lands in the US. In August 2021, we used the following search terms in the ISI Web of Science: (TI=title, TS=topic, \$=wildcard characters to include publications with alternative forms of the word): TI=(“pollinator\$” OR “bee\$” OR “butterfly” OR “butterflies” OR “fly” OR “flies”) AND TS=(“prescribed fire” OR “prescribed burn” OR “logging” OR “grazing” OR “invasive removal” OR “seed mix”) but NOT TS=(“honey bee\$” OR “agriculture” OR “beef”), to find previously published peer-reviewed primary literature for review. We searched for “prescribed burn” and “invasive removal” (as opposed to wildfires or presence of invasive species) to limit results to management actions. We omitted the topics “honey bee” and “agriculture” to restrict results to wild pollinator communities on public lands, and “beef” to exclude studies investigating pest control of flies on beef cattle. Studies that were not conducted strictly on public lands but in neighboring natural and semi-natural ecosystems were also included, because adjacent, non-federal lands have similar habitat characteristics and are sometimes managed to preserve the ecosystem services provided by public lands (i.e., “Good Neighbor Authority”). Results from the initial search string in the ISI Web of Science returned 399 studies. Studies were included in the review process if a publication was: (i) primary literature, (ii) conducted in the US, (iii) conducted in semi-natural or natural ecosystems, (iv) compared the response of pollinators

to experimental management actions between treatment and control groups, and (v) the focal taxa were bees (Hymenoptera: Apoidea), butterflies (Lepidoptera), and flower flies (Diptera: Syrphidae). Consequently, studies were excluded if they were: (i) reviews, meta-analyses, or opinions, (ii) conducted outside the US or in agricultural or urban ecosystems, (iii) did not include a control treatment, and (iv) investigated non-pollinating insects. We also searched for relevant studies meeting the same criteria within the reference section of studies found using the ISI Web of Science and Google Scholar. In total, 63 studies were included in the review process (Supplemental Table 2). Given that ‘honey bees’ were omitted as a search topic, studies related to the effects of commercial pollinators were found by searching keywords using Google Scholar (honey bee, pathogens, co-occurring).

Studies were categorized into groups depending on the experimental design as treatment v. control, observational, or combinations of management actions. Treatment v. control studies compared the response of pollinators to experimental treatments of a single management action and a control group. This group of studies was the most important group to determine the effects of management actions on pollinators. Observational studies reported results of an individual management action on pollinators without including an untreated control group. A final category investigated the interactive effects of management actions by comparing the response of pollinators to a combination of management actions to individual management actions; these studies also sometimes included untreated controls.

Calculating results

A result was defined as any comparison of the abundance, richness, or diversity for each taxon in a habitat type between treatment groups within a study. Occasionally, individual studies investigated multiple taxa, management actions, or habitat types, and produced multiple results. Management actions influenced pollinator communities if the abundance, richness, or diversity (Simpson’s or Shannon’s Diversity Index) of pollinators was significantly different (p -value < 0.05) between treatment groups. Results from each study were classified into positive, negative, or neutral effects on pollinators, which were then summed across all studies within a management action to determine an overall effect on pollinators (i.e., vote counting) (Supplemental Table 3). This ‘vote counting’ method was used, as opposed to a meta-analytic approach that estimates effect sizes and uncertainty, to accommodate small sample sizes, an uneven distribution of studies across land management actions, and highlight habitat-specific responses of pollinators to management actions. Some studies examined multiple taxa and/or management types and these studies contributed more than one result towards the overall count (Supplemental Table 3). Observational studies were not included in this analysis but are still included in this review to provide additional insights into the effects of management on pollinators. The effects of commercial pollinators on public lands was not considered land management. However, the question of whether commercially managed bees (honey bees and some bumblebees) belong on public lands is of great interest and we provide an overview of this topic.

Results

We compiled 63 individual studies investigating the effects of management on pollinators in natural and semi-natural ecosystems in the US (Supplemental Table 2). The number of studies varied depending on the management action, pollinator taxon, and habitat

type. Specifically, prescribed burning was the most studied management action (Fig. 2a), bees were the most studied taxon (Fig. 2b), and grasslands was the most studied habitat (Fig. 2c). Nearly all studies were published after the year 2000 (97%).

Prescribed burning

Prescribed burning was the most frequently studied management action. The effects of prescribed burning on pollinators have been investigated in a variety of taxa and habitat types but studies focus primarily on butterflies and are located in grassland ecosystems (Supplemental Table 4). When results were summarized across studies comparing treatment and control groups, prescribed burning had positive ($n=20$), neutral ($n=22$), or negative ($n=4$) effects on pollinator abundance, richness, or diversity when compared to unburned controls. Specifically, the effects of prescribed burning on abundance, richness, and/or diversity were either positive ($n=9$), or neutral ($n=12$) for bees; positive ($n=8$), neutral ($n=8$), or negative ($n=4$) for butterflies; positive ($n=2$), or neutral ($n=2$) for flies; and positive ($n=1$) for floral visiting insects (Fig. 3; Supplemental Table 3). Among observational studies, as time since burn increased, the abundance, diversity and/or richness declined ($n=3$) for bees, declined ($n=1$) for floral visiting insects, and increased ($n=3$) or remained the same ($n=1$) for butterflies.

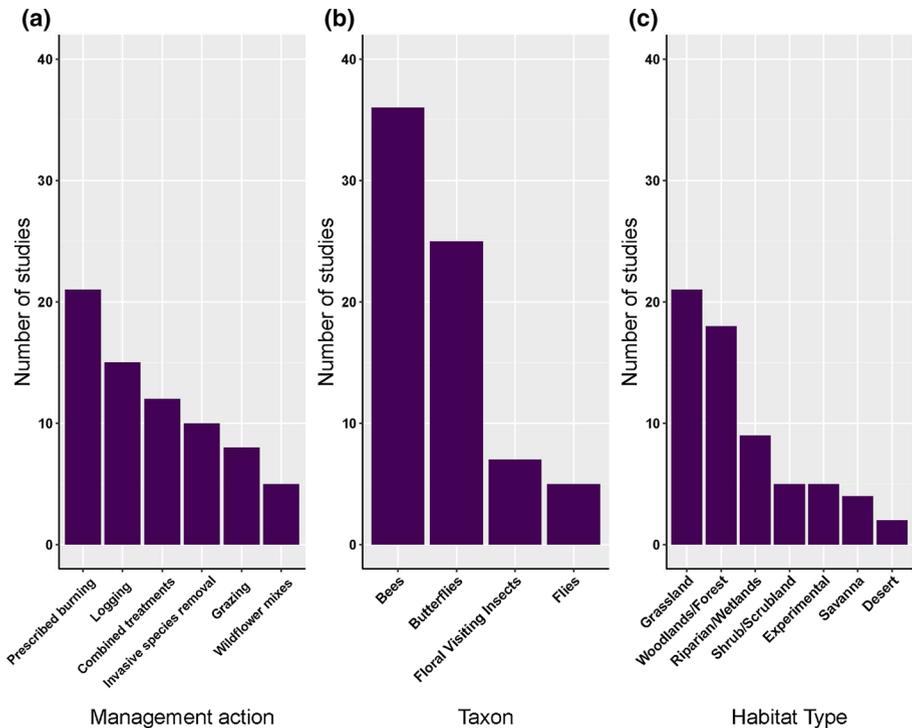


Fig. 2 The number of studies reporting results (y-axis) varied depending on the **a** management action, **b** taxon, and **c** habitat type, (x-axes)

Logging

Most studies investigating the effects of logging on pollinators were focused on bees and were conducted in woodlands/forest ecosystems (Supplemental Table 4). In no case, regardless of taxa or habitat type, were the effects of logging detrimental to pollinators. There was either a positive ($n=14$) or neutral ($n=20$) effect of logging on pollinator abundance, richness, and/or diversity when compared to unlogged controls. Specifically, the effects of logging on abundance, richness, and/or diversity were either positive ($n=10$) or neutral ($n=11$) for bees; positive ($n=2$) or neutral ($n=5$) for butterflies; positive ($n=1$) or neutral ($n=3$) for flower flies; and positive ($n=1$) or neutral ($n=1$) for floral visiting insects (Fig. 3; Supplemental Table 3). Among observational studies, three reported mixed effects of post-disturbance logging activities (salvage logging and residue removal) on bees, one demonstrated that bee abundance and richness declines with time since logging, and one demonstrated that bee abundance, richness, and diversity increases with logging intensity (Supplemental Table 3).

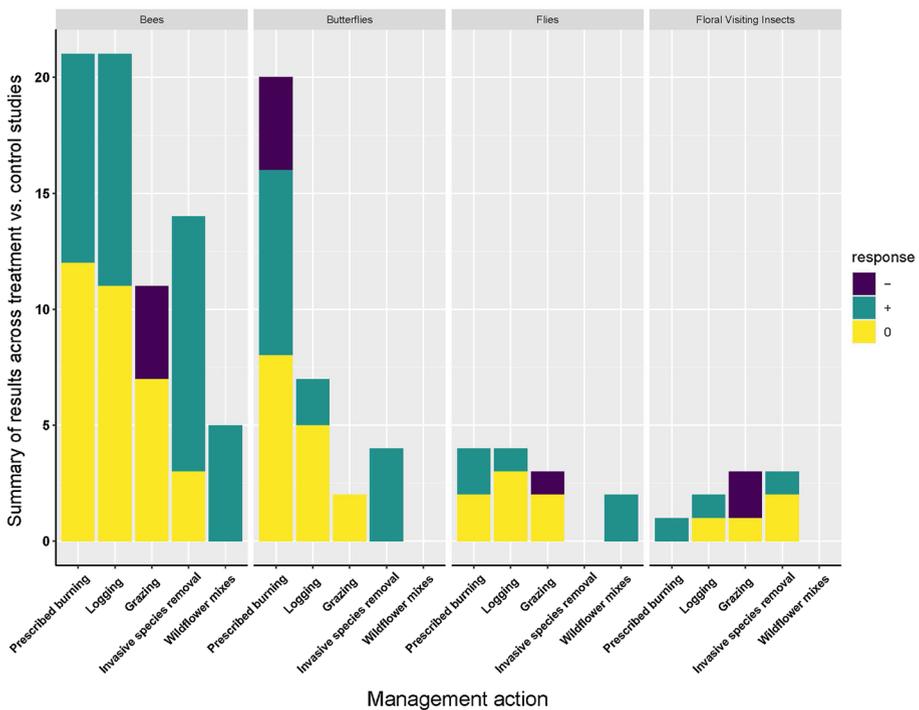


Fig. 3 The overall effects of each management action on pollinator abundance, richness, and/or diversity. A result was defined as any comparison of the abundance, richness, or diversity between treatment groups within a study. Results that compared pollinator abundance, richness, and/or diversity between treatment and control groups were summarized across all studies (y-axis) within a management action (x-axis), for each taxon (panels). Management actions potentially increased (+, teal), decreased (–, purple), or had no effect (0, yellow) on pollinator communities

Grazing

Studies investigating the effects of grazing on pollinators have primarily focused on bees and butterflies in grassland ecosystems in the Great Plains region of the US (Supplemental Table 4). Grazing had either negative ($n=7$) or neutral ($n=12$) effects on pollinator abundance, richness, and/or diversity when compared to ungrazed controls. Specifically, the effects of grazing on pollinator abundance, richness, and/or diversity were either negative ($n=4$) or neutral ($n=7$) for bees; neutral ($n=2$) for butterflies; negative ($n=1$) or neutral ($n=2$) for flower flies; and negative ($n=2$) or neutral ($n=1$) for floral visiting insects (Fig. 3; Supplemental Table 3). One observational study reported that bee diversity declines in response to increased grazing intensity and two observational studies reported negative or neutral effects of sheep grazing compared to cattle grazing on bee abundance (Supplemental Table 3). No studies investigated an effect of time-since-grazing to understand potential lag effects on pollinator communities and habitat structure.

Invasive species removal

There is an extensive body of literature on the effects of invasive species introductions on pollinators, but only ten studies have investigated the effects of invasive species removal on pollinators on public lands. Studies investigating the effects of invasive species removal on pollinators were largely focused on the effects of shrub removal on bees in wetland/riparian ecosystems (Supplemental Table 4). Removing invasive species had mostly positive ($n=16$) but also neutral ($n=5$) effects on pollinator abundance, richness, and/or diversity when compared to control groups. Specifically, the effects of invasive species removal on pollinator abundance, richness, and/or diversity were either positive ($n=11$) or neutral ($n=3$) for bees; positive ($n=4$) for butterflies; and positive ($n=1$), or neutral ($n=2$) for floral visiting insects (Fig. 3; Supplemental Table 3).

Revegetation with wildflower mixes

Public lands are composed of semi-natural and natural ecosystems, but most studies on the effects of revegetation with wildflower mixes on pollinators took place in experimental systems (Supplemental Table 4). Revegetating areas with wildflower mixes consistently had positive effects on bee ($n=5$) and flower fly ($n=2$) abundance and/or richness when compared to untreated areas (Fig. 3; Supplemental Table 3).

Combined management actions

In total, there were twelve studies that investigated the effects of combined management actions on pollinators (Supplemental Table 4). These studies were predominately located in grassland ecosystems which combine grazing and burning, or woodlands/forest which combine thinning and burning, to replicate historic patterns of disturbances across the landscape.

Five studies investigated the effects of combining thinning and burning on pollinators. The combination of thinning and burning had predominately positive ($n=16$) or neutral ($n=3$) effects on pollinator abundance, richness, and/or diversity when compared to untreated control groups (Supplemental Table 3). Four of the studies made direct

comparisons between a combination of logging and burning, and prescribed burning or logging alone. Of these studies, three found that prescribed burning or logging alone had no effect on pollinators but burning and logging combined had positive effects on bees ($n=3$), butterflies ($n=1$), and flower flies ($n=1$) (Supplemental Table 3).

Seven studies investigated the effects of combining burning and grazing to the individual effects of burning on pollinators. Six of these studies investigated the effects of a patch-burn grazing scheme (continuous grazing from cattle with rotational burning in the same patch) on pollinators. Of these studies, three found that prescribed burning alone did not influence butterflies, one found that prescribed burning increased Regal Fritillary (*Speyeria idalia*) abundance, and two found that burning did not affect bees, when compared to patch-burn grazing treatments (Supplemental Table 3). Furthermore, one study investigated the combination of burning and grazing (without a patch-burn scheme), and found that burning alone decreased butterfly abundance, but increased diversity, when compared to burning and grazing (Supplemental Table 3).

Discussion

Prescribed burns

While there were predominately neutral or positive effects of prescribed burns on bee and butterfly richness, abundance, and diversity (20 positive, 22 neutral, 4 negative), occasional negative effects of prescribed burns on butterflies suggest that burning can have mixed effects for pollinator conservation on public lands. Additionally, studies were primarily conducted in woodlands/forest, shrub/scrublands and savanna habitat types, which are fire-prone ecosystems in which pollinators might be adapted to fire. Consequently, prescribed burning may have species- and habitat-specific effects on pollinators throughout public lands in the US.

Prescribed burns are thought to mimic wildfires and positively influence pollinators by creating early seral stage habitats with abundant floral resources, coarse woody debris, and bare ground (Carbone et al. 2019; Potts et al. 2003; Simanonok and Burkle 2019), but we observed an equivalent number of positive and neutral effects, suggesting that prescribed burns frequently have no effect on pollinators in some circumstances or ecosystems. Bee abundance increased following burns in longleaf pine savannas (Moylett et al. 2020; Ulyshen et al. 2021), southern Appalachian hardwood forests ((Campbell et al. 2018), but see (Campbell et al. 2007)), and tallgrass prairies, along with increasing butterfly richness and diversity in upland forest and riparian habitats (Huntzinger 2003), abundance in oak pine woodlands (Rudolph et al. 2006), and tallgrass prairies (Panzer and Schwartz 2000). Prescribed burns also increased pollinator visitation rates to plants in southeastern old-fields (Van Nuland et al. 2013), and pollination services to the netted pawpaw (*Asimina reticulata*) in Florida scrubland (Barton and Menges 2018). However, prescribed burns have lower intensities compared to wildfires and are commonly conducted in already open habitats, potentially resulting in neutral effects on pollinators (Carbone et al. 2019). For instance, bee abundance and richness were not affected by prescribed burns in midwestern oak savannas (Lettow et al. 2018) or pinyon-juniper woodlands (Nyoka 2010) and had no effects on butterflies in Appalachian hardwood forests (Campbell et al. 2007, 2018). Burning during the growing season (spring and summer) in tallgrass prairies (Decker and Harmon-Threatt 2019), and burning in three to six year intervals in southern Appalachian

hardwood forests (Campbell et al. 2018) and longleaf pine savannas (Moylett et al. 2020; Ulyshen et al. 2021) appear to benefit pollinator communities in these habitat types.

Occasional negative effects of prescribed burning on butterflies suggests that prescribed burning may not always be consistent with pollinator conservation on public lands. Prescribed burns had species-specific effects on butterflies in sagebrush steppe (McIver and Macke 2014), tallgrass prairies (Moranz et al. 2012; Swengel 1996, 1998), and riparian corridors (Fleishman 2000). Furthermore, prescribed burns can result in local extirpations of specialists that require mature habitat in tallgrass prairie and shrubland ecosystems, especially when burning happens frequently (Powell et al. 2007; Swengel 1996, 1998; Swengel and Swengel 2001, 2007; Vogel et al. 2010). In some situations, butterfly populations could benefit from burns conducted in three to five-year intervals (McCullough et al. 2019; Vogel et al. 2010; Warchola et al. 2018), during cool, and humid days (Hill et al. 2017), and by preserving mature habitats or the preferred food resources for caterpillars. Further work is required to resolve the taxa- and habitat-specific effects of prescribed burning on pollinators before it can be used as a tool for pollinator conservation on public lands.

Logging

Most studies that we reviewed reported a positive or neutral effect of logging on pollinators (14 positive, 20 neutral, 0 negative). As expected, logging studies almost always took place in woodlands/forest habitat types but occasionally logging was conducted within shrub/scrublands and savanna as a method to counteract woody plant invasion. Pollinator abundance and diversity declined as time-since-logging increased and was often greatest in clear cut forests, indicating logging return intervals and severity should be considered to support pollinator communities in forested habitats. Furthermore, post-disturbance logging activities had mixed effects on pollinators and more research is required to understand the influence of management actions on landscape legacies.

Logging regimes that create gaps in the canopy may benefit pollinators by increasing nutrient flux, light availability, primary productivity, and floral resource availability at the forest floor (Korpela et al. 2015; Waltz and Wallace Covington 2004). Recent logging had positive and neutral effects on pollinator abundance and richness in southern Appalachian hardwood forests (Campbell et al. 2007, 2018; Jackson et al. 2014; Mullally et al. 2019), and on bee abundance, richness, and diversity in northeastern hardwood forests (Roberts et al. 2017; Romey et al. 2007) when compared to unlogged stands. Bee abundance and richness were greatest immediately following logging but declined within five years in mixed-conifer forests (Rivers and Betts 2021). Additionally, bee abundance and richness were greatest within clear-cut stands compared to more selective logging practices in hardwood forests of the eastern US (Romey et al. 2007), but group selection logging (Proctor et al. 2012; Roberts et al. 2017), variable retention logging (retaining a proportion of standing trees during logging to conserve forest structure) (Romey et al. 2007), as well as thinning in pine savanna (Breland et al. 2018), pine shrubland (Kleintjes et al. 2004), and southern Appalachian hardwood forests (Campbell et al. 2018; Mullally et al. 2019) still benefited bee and butterfly communities when compared to unlogged forests. However, mowing to remove woody plant species in scrub-oak woodlands (Bried and Dillon 2012), or thinning in a pinyon-juniper woodland had no effect on pollinators (Nyoka 2010). Managers may consider less-intensive logging strategies to avoid soil compaction, the introduction of invasive species, and edge effects (Lindenmayer and Franklin 2002), to provision timber while generating canopy gaps for pollinators in forested ecosystems.

Post-disturbance logging activities, like salvage logging and harvesting logging residue, are conducted on public lands to meet the growing demand for timber and energy but may remove nesting substrates for dead wood dependent taxa (Thorn et al. 2018). Following wildfires, salvage logging recovers useable wood, accelerates the establishment of trees, and reduces fuels that contribute to severe wildfires (Lindenmayer and Noss 2006). In Oregon mixed-conifer forests, salvage logging following high-severity fires decreased bee richness compared to wildfire alone (Galbraith et al. 2019), but salvage logging following mixed-severity fires in Montana increased bee richness and did not influence the proportions of cavity-nesting individuals or species (Heil and Burkle 2018), suggesting that the effects of salvage logging on bees may be contingent on wildfire severity. However, the benefits of salvage logging for bee communities following mixed-severity fires did not improve the delivery of pollination services to a common shrub (*Symphoricarpos albus*) (Heil and Burkle 2018, 2019). Additionally, following logging, woody biomass residues can be collected as a fuel for energy production (Gan and Smith 2006). Harvesting logging residue increased ground-nesting species abundance and richness once enough material was removed from the forest floor to expose bare ground (Rivers et al. 2018b). Future work may investigate the effects of post-disturbance logging following bark beetle outbreaks, which benefit pollinators by opening the canopy (Davis et al. 2020; Foote et al. 2020), but increase fuels that can contribute to catastrophic wildfires.

Grazing

Studies reported mostly neutral and negative effects, but never positive effects, of grazing on pollinator abundance, richness, and diversity (0 positive, 12 neutral, 7 negative), suggesting grazing potentially threatens pollinator health on public lands. Furthermore, grazing had a neutral effect on pollinators in grasslands of the Great Plains, but a negative effect in other regions of the US, highlighting that pollinators within grazing-adapted ecosystems may be resilient against herbivory from ungulates. Consequently, the interaction between the domestic ungulate species and habitat type may influence pollinator communities on public lands in the US.

Intensive grazing can pose threats to pollinators by trampling bee nesting structures, consuming floral resources, and converting vegetation communities into “grazing lawns” which are dominated by plants with functional traits that can withstand grazing pressures, like grasses (Black et al. 2011). Intensive grazing from cattle reduced bee abundance and richness compared to ungrazed areas in deserts (Minckley 2014) and montane wetlands (Hatfield and LeBuhn 2007), along with pollinator diversity in semi-arid grasslands (DeBano 2006; Kimoto et al. 2012). Conversely, grazing ungulates at low to intermediate intensities in grazing-adapted ecosystems can restore historic disturbance regimes, maintain ecosystem structure, and increase pollinator abundance (Lazaro et al. 2016; Shapira et al. 2020; Tonietto and Larkin 2018; Vulliamy et al. 2006). While we found no studies that reported a positive effect of grazing on pollinators, low intensity grazing regimes had no effect on butterfly richness in a flooded grassland (Elmer et al. 2012) and grazing had no effect on populations of the Regal Fritillary (McCullough et al. 2019) or bee abundance, richness, and diversity (Stein et al. 2020) in a tallgrass prairie ecosystem. Managers may consider ways to reduce grazing pressure from ungulates by using fences (Cole et al. 2015) or excluding grazers from areas when flowers are blooming (Davis et al. 2014; DeBano et al. 2016), in order to conserve pollinator habitats while grazing cattle on rangelands in the US.

Species-specific grazing regimes of wild and domestic ungulates may have differential effects on pollinators on public lands. Sheep grazing had a negative effect on bumble bee abundance when compared to cattle grazing in montane grasslands (Hatfield and LeBuhn 2007), but following burns, the combination of sheep and cattle grazing did not influence butterfly abundance when compared to cattle-only grazing (Ogden et al. 2019). Consequently, the effects of sheep grazing on pollinators could be mitigated by other management actions that improve vegetation communities. While no study investigated the effects of wild ungulate grazing on pollinators, land managers may modify densities of elk (*Cervus* spp.), deer (*Odocoileus* spp.), pronghorn (*Antilocapra americana*), moose (*Alces alces*), and bison (*Bison bison*) to expand hunting opportunities on public lands with unknown consequences for pollinators. Wild ungulates have diets that overlap with bee species (DeBano et al. 2016), reduce population abundance of flowering plants (Knight 2004), and potentially remove plant species required by butterflies for ovipositing (Debinski 1994; Smallidge and Leopold 1997). Conversely, wild ungulates are less constrained to rangelands and may induce rotational grazing patterns through migratory behaviors, with potential benefits for vegetation communities (Stewart et al. 2002). Studies using multiple ungulate species are needed in woodland/forest, shrub/scrubland, and savanna habitat types to comprehensively understand the effects of grazing on pollinators throughout rangelands in the US.

Invasive plant species removal

While many studies have explored the effects of invasive species introduction on pollinators (Charlebois and Sargent 2017), few studies have investigated the effects of invasive species removal on pollinators. Results from our literature search suggest that invasive species removal had a positive effect on both bee and butterfly taxa (16 positive, 5 neutral, 0 negative), but studies were dominated by shrub removal in a riparian/wetland system from the eastern US (Fiedler et al. 2012; Hanula and Horn 2011; Hudson et al. 2013; McKinney and Goodell 2010; Ulyshen et al. 2020). Management actions that consistently benefit pollinators in some habitats can be implemented for pollinator conservation on public lands.

While invasive shrub removal in the eastern US clearly benefits pollinators, removal of plants from the understory has inconsistent effects on pollinators. Invasive shrubs that occupy the middle canopy layer can reduce the amount of light and temperature at the forest floor, which decreases the productivity of native floral species and the metabolism of pollinators (McKinney and Goodell 2010). Consequently, removing invasive shrubs increased bee and butterfly abundance and richness at the forest floor in wetlands (Fiedler et al. 2012), riparian forests (Hanula and Horn 2011; Hudson et al. 2013; Ulyshen et al. 2020), and deciduous forests (McKinney and Goodell 2010) in multiple locations in the eastern US. The positive effects of invasive shrub removal on bee and butterfly communities persisted within riparian forests for at least five years following treatments (Hudson et al. 2013). However, invasive flowering plants can become preferred resources for pollinators (Lopezaraiza-Mikel et al. 2007; Vila et al. 2009), can increase, decrease, or have no effect on pollinator visitation to co-occurring native plant species depending on floral traits (Charlebois and Sargent 2017), and can extend the duration of the growing season if invasive species bloom later in the summer than native species (Herron-Sweet et al. 2016). Trimming flowers to simulate invasive species removal increased (Baskett et al. 2011) and had no effect on pollinator visitation to co-occurring plant species (Chung et al. 2014; Goodell and Parker 2017), which is similar to the inconsistent effects of removing invasive

flowering plants on plant-pollinator interactions (Charlebois and Sargent 2017). Future work is required to disentangle the effects of removing plants that have already established and formed complex interactions with pollinator communities (Biella et al. 2019; Zavaleta et al. 2001).

The response of pollinators to herbicide application, natural enemies, and mechanical removal may determine which management actions are effective for invasive species removal and pollinator conservation on public lands. When applied directly to bees within cages, herbicides increased bee mortality, potentially because surfactants within herbicide mixtures blocked gas exchange (Straw et al. 2021), however this has yet to be tested within a field setting. Applying herbicides can also have non-target effects on native forb communities, potentially reducing floral resources for pollinators and leading to secondary invasions of nonnative plants (Pearson et al. 2016). To avoid non-target effects of herbicides on native plant communities, land managers often use natural enemies of plants, which can reduce invader abundance and modify pollinator behavior to limit pollen deposition and seed production of invasive plants by altering the floral display (Cariveau and Norton 2014; Swope and Parker 2012) and scent (Burkle and Runyon 2016). However, studies have only examined the effects of biocontrol on pollinator visitation to the target plant species, instead of the influence of biocontrol on the wider pollinator community. Furthermore, machine mulching and hand-felling invasive trees in riparian forests were equally effective at increasing bee and butterfly abundance and richness (Hanula and Horn 2011). Future work might investigate methods like prescribed burns to remove invasive plant species and encourage the regrowth of native plant communities to support pollinators.

Revegetation with wildflower mixes

Wildflower mixes are a combination of plant species designed to establish vegetative cover, prevent soil erosion following disturbances, supplement forage for ungulates, and provide floral resources for pollinators (Harmon-Threatt and Chin 2016). Studies investigating the effects of revegetating landscapes with wildflower mixes reported a clear positive effect on pollinator abundance, richness, and diversity (7 positive, 0 neutral, 0 negative). However, our literature search only identified five studies, which were primarily conducted in experimental settings. Revegetating public lands with flowering plants may be an effective tool to restore pollinator communities and achieve multiple management goals on public lands.

Within an experimental system, bee and syrphid fly abundance and richness increased as the area established with wildflowers also increased (Blaauw and Isaacs 2014b). The establishment of native plants increased visitation rates and fruit-set of blueberry plants in adjacent fields (Blaauw and Isaacs 2014a) and a plant of conservation concern (*Deinandra minthornii*) in a large-scale remediation project (Galea et al. 2016), suggesting that native plants established through management actions support plant and pollinator community restoration and increase floral resources for pollinators. Furthermore, within tallgrass prairie, soil temperature, the amount of bare ground, and potential nesting sites for ground-nesting bees was greater in sites seeded with high diversity mixes compared to low-diversity mixes (Anderson and Harmon-Threatt 2016), potentially because native plants exclude grasses and have complex root structures that improve soil health. However, a seed mix designed for habitat revegetation at large spatial scales in the Great Basin primarily contained flowering plants that were not attractive for pollinators (Cane and Love 2016), suggesting that the plants available to land managers for restoration in semi-natural areas may not be the most effective for pollinator restoration. Future work may observe pollinator

visitation to plant species within a restoration context to identify plant species that are the most attractive to pollinators and design seed mixes that are effective for pollinator restoration on public lands (Burkle et al. 2020; Glenny et al. 2022; Harmon-Threatt and Hendrix 2015; Williams and Lonsdorf 2018).

Hosting commercial pollinators

Honey bees (*Apis mellifera*) and some bumble bees (*Bombus* spp.) are managed to provide pollination services for agricultural crops and generate revenue for beekeepers from honey production, but high population densities of managed bees could increase competition for resources (Mallinger et al. 2017) and share pathogens with native bees (Grozinger and Flenniken 2019; Tehel et al. 2016). Public lands are important for storage and pesticide-free forage for honey bees between crop seasons (Otto et al. 2018). While the direct effects of bee pathogens on native bee fitness and survival remain unknown, population declines of North American bumble bees are correlated with detections of the fungal pathogen *Nosema bombii* since the mid-1990s (Cameron et al. 2016). Vegetation management and selection of plants for seed mixes might consider prioritizing plants with antimicrobial properties to increase the abundance of foraging resources that protect wild bees from pathogens found in commercial bee species (Adler et al. 2020; Giacomini et al. 2018; Richardson et al. 2015). Future research may understand how vegetation communities can mitigate competition for floral resources and pathogen transmission between commercially managed species to conserve wild bee communities on public lands. Moreover, regulating wild bee trapping on public lands (e.g., blue orchard bees, *Osmia lignaria*) and transportation to agricultural systems may be required to avoid depleting wild bee populations (Tepedino and Nielson 2017). Reducing the presence of commercial pollinators on public lands will likely reduce competition and pathogen transmission between pollinator species.

Combinations and interactions between multiple management actions

The combinations of logging and burning were required to benefit pollinator communities on public lands in three of the four studies. While logging and prescribed burns alone had no effect on pollinators, the combination of logging and burning benefitted pollinators in Appalachian hardwood forests (Campbell et al. 2007), pinyon-juniper woodlands (Nyoka 2010), and oak savanna (Lettow et al. 2018). However, in areas of Appalachian hardwood forests where burns were repeated in three to six-year intervals, the combination of thinning and prescribed burning had a similar effect as singular management actions on pollinator communities (Campbell et al. 2018). Furthermore, combining logging and burning may be used as a restoration tool to increase canopy gaps, and restore historic fire regimes, which benefits butterflies in desert pine forests (Waltz and Wallace Covington 2004). Combining management actions may influence local habitat characteristics and provide resources for pollinator communities with diverse habitat requirements at a landscape scale (Griffin et al. 2021).

The combined effects of burning and grazing may be used without major effects on pollinator populations in grasslands. The combination of burning and grazing with cattle increased butterfly abundance, but decreased diversity when compared to burning alone in tallgrass prairie (Vogel et al. 2007). Tallgrass prairies managed under a patch-burn management strategy had no effect on bee and butterfly species richness and abundance or the nutritional value of plant communities for pollinators when compared to burn only (Bendel

et al. 2018; Buckles and Harmon-Threatt 2019; Debinski et al. 2011; Moranz et al. 2012; Moranz et al. 2014; Smith et al. 2016), suggesting tallgrass prairies that are burned can support domestic ungulates without direct effects to pollinator communities. However, soil suitability for pollinators declined after multiple years of patch-burn grazing, when compared to burning alone, suggesting managers may consider withholding grazing some years to protect belowground nesting resources for pollinators (Buckles and Harmon-Threatt 2019). Future studies may develop restoration strategies that can be paired with management actions that have a negative effect on pollinator communities.

Landscape features to support pollinator connectivity

Managers may consider constructing pollinator movement corridors to support healthy plant and pollinator populations (Townsend and Levey 2005; Van Geert et al. 2010). Pollinators with limited flight distances are potentially restricted in their ability to disperse into new habitats (Bartomeus et al. 2013; Bommarco et al. 2010; Hopfenmüller et al. 2014). To enable pollinators to recolonize areas following management actions, managers may consider improving roads and powerline easements with floral resources to create pollinator-friendly corridors (Townsend and Levey 2005; Van Geert et al. 2010). Roads and powerlines are marginal and open habitats with higher light availability, foraging resources, and consequently species-rich bee communities (Hopwood 2008; Russell et al. 2018; Steinert et al. 2020; Wagner et al. 2019). While floral resources along roadways can attract bees and butterflies to areas of high vehicle-induced mortality (Baxter-Gilbert et al. 2015; Keilsohn et al. 2018), pollinators may be reluctant to cross wide roads (Fitch and Vaidya 2021). Defining characteristics of roads that decrease pollinator mortality could be important to identify where pollinator movement corridors can be installed to support healthy pollinator populations.

Conclusion

Public lands are among the most valuable habitats for pollinators in the US, but increased pressure to provide various ecosystem services requires management that is consistent with pollinator conservation. Seed mixes and invasive shrub removal had overwhelmingly positive effects on pollinators. Burning can benefit bees in some habitats (e.g., longleaf pine savannas) but have a negative effect on some specialist butterflies in tallgrass prairie, suggesting research may investigate aspects of burning regimes in different ecosystems that protect pollinators before fire can be applied as a management tool. Logging had mostly positive effects on pollinators resulting from creating gaps in the canopy, suggesting management actions that generate canopy openings, like burning in forests, logging, or invasive shrub removal, are important to improve habitat suitability for pollinator communities. Additionally, grazing had no effect on pollinators in ecosystems evolutionarily adapted to ungulates, but a negative effect on pollinators in other habitats around the US, implying that managers may consider excluding cattle from pollinator habitat in some ecosystems. Furthermore, commercially managed pollinators co-foraging with wild bees may result in pathogen transmission and competition for resources. The combination of thinning and burning or burning and grazing may be required to conserve pollinators, while meeting multiple management goals on public lands. Facilitating the movement of pollinators into habitat patches can be achieved by improving roads and powerline corridors with floral

resources. Management actions on public lands can be compatible with insect pollinator conservation, but research is still required to effectively apply management actions across ecosystems and accomplish multiple management goals.

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